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HOLOCENE CARBON DYNAMICS AND ATMOSPHERIC RADIATIVE FORCING OF DIFFERENT TYPES OF PEATLANDS IN FINLAND

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ACADEMIC DISSERTATION

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CONTENTS

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This thesis is based on the following publications, referred to in the text by their Roman numerals:

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III PJH Mathijssen, N Kähkölä, J-P Tuovinen, A Lohila, K Minkkinen, T Laurila, M Väliranta (*submitted to Journal of Geophysical Research: Biogeosciences*) Millennia-long climate warming impact after initiation of a boreal peatland in Finland driven by lateral expansion and low carbon accumulation rates.

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AUTHOR'S CONTRIBUTIONS TO THE PUBLICATIONS

I The study was planned by M. Väliranta, and A. Lohila. E. Niemelä, A. Lohila and M. Väliranta were responsible for the collection of peat samples. E. Niemelä performed peat analyses under the supervision of M. Väliranta. A. Lohila, M. Aurela and T. Laurila were responsible for carbon flux data and T. Laurila financed the radiocarbon analyses. P. Mathijssen analysed and combined the collected data and performed radiative forcing modelling together with J.-P. Tuovinen. P. Mathijssen was responsible for writing the manuscript, with contributions from M. Väliranta, E-S. Tuittila, A. Lohila, S. Juutinen and J-P. Tuovinen.

II The first step of the study was planned by E-S. Tuittila and M. Väliranta. A Master's student; A. Miettinen implemented the coring with the assistance of P. Alekseychik, and measured the bulk density of the samples under the supervision of E-S. Tuittila. The study plan was later extended with P. Mathijssen and A. Korrensalo. P Mathijssen was responsible for the collection of peat samples, together with P. Alekseychik, A. Korrensalo, M. Väliranta and E-S. Tuittila. P. Mathijssen analysed the samples. A. Korrensalo measured and analysed methane flux data. P. Alekseychik, T. Vesala and J. Rinne provided eddy-covariance carbon flux data and T. Vesala financed the radiocarbon analyses. P. Mathijssen analysed the collected data with contributions from E-S. Tuittila, and prepared the manuscript with contributions from all co-authors.

III The study was planned by P. Mathijssen, A. Lohila, K. Minkkinen and M. Väliranta. P. Mathijssen and a Master's student; N. Kähkölä collected the peat cores. P. Mathijssen and N. Kähkölä analysed the peat samples. T. Laurila and K. Minkkinen financed the radiocarbon analyses. P. Mathijssen combined and analysed the collected data, and performed radiative forcing modelling with J-P. Tuovinen P. Mathijssen prepared the manuscript with contributions from all co-authors.

ABSTRACT

Peatlands contain approximately a third of all soil carbon (C) globally and as they exchange carbon dioxide (CO_2) and methane (CH_4) copiously with the atmosphere, changes in peatland C budgets have a large impact on the global C balance and on the concentration of greenhouse gases in the atmosphere. How peatlands will react to future climate changes, however, is still relatively uncertain and as such there has been a growing interest in the reconstruction of past peatland C dynamics and linking these to past climate variations. In order to increase the understanding of peatland development and response patterns, I quantitatively reconstructed the Holocene (the last c. 11700 years) C dynamics of three different peatlands in Finland: a subarctic rich fen, a boreal poor peatland complex and a boreal managed pine bog. Several cores from each peatland were studied in order to reconstruct peatland succession, lateral expansion, peat and C accumulation rates, long term uptake of atmospheric CO_2, CH_4 fluxes and radiative forcing (RF).

Peatland lateral expansion was most rapid during periods with relatively cool and moist climate conditions. The peatlands showed distinct successional pathways, which were sometimes triggered by fires. Successional stages were partly reflected in C accumulation patterns. In some cases, variations in C accumulation rates coincided with autogenic changes in peat type and vegetation, although accumulation rates were also related to the large-scale Holocene climate phases. The warm and dry conditions during the Holocene Thermal Maximum (between c. 9000 and 5000 years ago) reduced C accumulation rates in the subarctic fen and the boreal peatland complex. Reconstructed CH_4 emissions suggest that CH_4 emissions played a major role in the total C budget of the peatlands throughout the Holocene. The RF models based on long term CO_2 uptake and CH_4 emissions showed that the two boreal peatlands had a warming effect on the atmosphere for the first 4000-7000 years after the start of peat accumulation, after which they had an increasing cooling effect as a result of the long term effect of C uptake and storage. In contrast to the two southern sites, the subarctic fen had a warming effect through its entire history as a result of very low C accumulation rates.

The results of my study show that peatland processes react differently to allogenic factors, such as climate and fire, depending on peatland type, microtopography and local hydrology. It highlights the necessity to study multiple peat cores per site before making exhaustive conclusions on historical development patterns and implications. The combination of lateral and vertical peat growth data with reconstructed CO_2 and CH_4 fluxes provided the necessary information for a comprehensive quantification of the climate - peatland feedback. In the studied sites this feedback seemed to be very sensitive to short term variations in CH_4 emissions and lateral expansion.

ABBREVIATIONS

BD	dry bulk density of peat samples (g cm^{-3})
C	carbon
cal. BP	calibrated years before present (present = 1950 AD)
CAR	carbon accumulation rate (g C m^{-2} a^{-1})
CCA	canonical correspondence analysis
CO_2	carbon dioxide
CH_4	methane
DOC	dissolved organic carbon
GWP	global warming potential
HTM	Holocene Thermal Maximum
ka BP	thousand years before present (present = 1950 AD)
LOI	loss on ignition (%)
RF	radiative forcing (W m^{-2})
WA	weighted averaging

1 INTRODUCTION

1.1 ROLE OF PEATLANDS IN GLOBAL CARBON BALANCE

Peat is partially decomposed organic material that has accumulated over time. It is mainly composed of dead plant material that contains various types of plant remains: wood, leaves, rhizomes, and bryophytes, especially the so called peat mosses in the genus *Sphagnum* (Clymo, 1983). In peatlands, the plant litter does not decompose completely, because the anoxic conditions in the water saturated soil severely limit the activity of decomposing microbes (Clymo, 1984). Therefore, peatlands are efficient long term carbon (C) sequestering ecosystems. In addition to the prevailing anoxic conditions, peat plants often contain recalcitrant substances that are resistant to decomposition (Børsheim et al., 2001). In addition, the pore water in peatlands tends to have a low pH, and this reduces the rate of decomposition (Clymo and Hayward, 1982).

Peatlands occur under a wide variety of conditions, as long as there is a positive moisture balance (Rydin and Jeglum, 2006). Peatlands can be found in the tropics, temperate, boreal and arctic regions of both northern and southern hemispheres. However, northern peatlands, located at high latitudes in America, Europe and Asia, comprise c. 90% of the global peatland area (Yu, 2011). All northern peatlands combined have accumulated approximately 500 Pg C (Pg = 10^{15} g) during the Holocene (the last c. 11700 years), which is c. 90% of the total C pool stored in peatlands globally (Yu, 2011; Loisel et al., 2014). This amount is equivalent to c. 30% of the present global soil C, and nearly equal to the pre-industrial atmospheric C reservoir (Yu, 2012). Consequently, northern peatlands play a prominent role in the global C balance. Although peatlands are effective C sinks through the uptake of atmospheric carbon dioxide (CO_2), they are also an important source of methane (CH_4) (Turetsky et al., 2014; Petrescu et al., 2015). CH_4 emissions represent up to 25% of the net ecosystem C balance of peatlands (Limpens et al., 2008).

As a result of the simultaneous uptake of CO_2 and emissions of CH_4, peatlands have a dualistic influence on the atmospheric greenhouse effect, so called climate forcing (Frolking and Roulet, 2007; Korhola et al., 2010; Yu, 2011). This effect can be expressed as radiative forcing (RF) that quantifies the change in net irradiance at the top of the troposphere (Myhre et al., 2013). The current RF of northern peatlands, where CO_2 storage and CH_4 emissions over the Holocene are incorporated, has been estimated to be between -0.22 and -0.56 W m^{-2} (Frolking and Roulet, 2007). A negative value indicates a cooling impact on the atmosphere. The magnitude of this cooling impact is equivalent to approximately 10 to 25% of the anthropogenic climate warming since pre-industrial times; +2.3 W m^{-2} (IPCC, 2014). However, the C fluxes of peatlands vary through time in relation to peatland growth in both vertical and horizontal directions (Korhola, 1994). This is related to the successional stages that peatlands go through (Tolonen, 1987; Svensson, 1988; Tolonen and Turunen, 1996). Moreover, variation in climate conditions have influenced peatland C dynamics (Gorham, 1991; Dorrepaal et al., 2009; Fan et al., 2013). Consequently, peatland climate forcing also varies through time. Accordingly, climate change is predicted to influence the C dynamics of northern peatlands (Gong et al., 2013), possibly accelerating or slowing down further changes due to climate - peatland feedback loops (McGuire et al., 2009).

1.2 PEATLAND CARBON DYNAMICS

Northern peatlands can be broadly divided into fens (minerotrophic peatlands) and bogs (ombrotrophic peatlands). Fens are peatlands that are predominantly fed by ground and surface waters containing dissolved minerals, whereas bogs mainly receive their water from precipitation (Wheeler and Proctor, 2000). In addition to hydrology, other environmental factors influence peatland functioning, and therefore, their C balance as well. These factors include local climate, underlying and surrounding substrate, topography, regional flora and the presence of permafrost (Vitt, 2006).

Autogenic processes are an important factor in peatland development. An example is vertical peat growth, which results in a decrease in pH and nutrient levels when the influence of precipitation is greater than the influence of minerogenic water flows. These autogenic processes result in successional changes in vegetation structure and water table depth (Hughes, 2000; Tuittila et al., 2013). Consequently, this may lead to a transition from fen to bog (ombrotrophication). The development of successional stages in northern peatlands is illustrated by the fact that young peatlands are predominantly fens, while a large part of older peatlands are bogs. The northernmost peatlands, north of c. 62 °N latitude in Finland, have mostly remained as fens since peatland initiation thousands of years ago, whereas in more southern boreal regions, fens have been transformed to bogs through ombrotrophication (Eurola et al., 1984). Fens are characterised by sedge-dominated vegetation, high CH_4 emissions and relatively low C accumulation rates (Tolonen and Turunen, 1996; Alm et al., 1999a; Drewer et al., 2010; Leppälä et al., 2011). C accumulation accelerates after ombrotrophication (Tolonen and Turunen, 1996; Drewer et al., 2010) and this is due to decreased decomposition rates, which is partly related to an increase in the proportion of *Sphagnum*, increased acidification and changes in water table levels (Hughes, 2000; Loisel and Yu, 2013a; Tuittila et al., 2013). In addition, ombrotrophication results in decreased CH_4 emissions (Turetsky et al., 2014).

The fluxes of CO_2 and CH_4 between peatland and atmosphere are closely linked to vegetation composition, in particular through differences between plant species and their productivity and litter decomposability (Moore and Knowles, 1989; Moore et al., 1990; Yavitt et al., 1997; Leppälä et al., 2008, 2011; Laine et al., 2012). Furthermore, the vegetation partly control CH_4 transportation pathways from the peat layers to the atmosphere and may provide microhabitats for the microbial communities responsible for CH_4 oxidation (Bellisario et al., 1999; Larmola et al., 2010). Fennoscandian ombrotrophic peatlands often display a vegetation gradient where the mire centre is occupied by bog or poor fen species, and rich fen species become more common towards the margins (Malmer, 1986; Økland et al., 2001). This gradient is suggested to be a consequence of increasing surface water flow towards the margins, resulting in higher uptake and turnover rates of limiting nutrients, as well as the increased influence of the mineral soil under a thinner peat layer (Ingram, 1967). The differentiation between mire centre and margin can also be observed in C accumulation patterns (e.g. Korhola et al., 1995; Mäkilä, 1997; Waddington and Roulet, 2000) and CH_4 emissions (Dise et al., 1993; Alm et al., 1999a). This means that lateral peatland expansion, which extends the peat margin outwards, will form new peat areas with temporarily high CH_4 emissions and low C accumulation rates (Korhola et al., 1996).

Important allogenic factors that regulate peatland C dynamics to a great extent are climatic conditions (Gorham, 1991; Dorrepaal et al., 2009; Fan et al., 2013). Climate warming might result in increased C uptake by peatlands, especially in bog environments, if the effective moisture regime remains within the required climate envelope (Charman et al., 2013; Loisel and Yu, 2013a). However, if the moisture balance does not remain positive, the increased decomposition will reduce the effect of accelerated primary production (Alm et al., 1999b; Ise et al., 2008; Dorrepaal et al., 2009). As CH_4 emissions are influenced by temperature and moisture conditions (Waddington et al., 1996; Alm et al., 1999b; Bellisario et al., 1999; Walter and Heimann, 2000), they are sensitive to changes in climate. Due to the profound differences in fen and bog dynamics these two peatland types can be expected to respond in different ways to changes in climate (Alm et al., 1997; Weltzin et al., 2000; Updegraff et al., 2001; Gong et al. 2013).

In addition to autogenic and natural allogenic processes, peatlands have been affected by land use activities. Drainage for forestry has affected approximately 5% of the total northern peatland area (Laine et al., 2009). However, at regional scales the proportion can be much higher. In Finland, for example, 55% and c. 5.7 million ha of peatlands have been drained for forestry during the last century (Turunen, 2008). Water table depth increases as a result of drainage and causes changes to the vegetation, namely a replacement of sedges and peat mosses by trees and forest mosses (Laine et al., 1995). Inevitably, drainage alters the factors that control the peatland C balance by changing, for example, rates of plant productivity, litter quality, activity of decomposing organisms and residence time of organic matter in aerated conditions (Laiho, 2006). In Finland, drainage for forestry has typically resulted in only a limited lowering of the water table (< 40 cm) and thus, in these sites, C sequestration has increased since drainage (Minkkinen and Laine, 1998; Alm et al., 1999a; Minkkinen et al., 2002). Whether drained peatlands change from C sinks to sources in the long term, however, depends on peatland type, local climate and the extent of change in water level (Laiho, 2006; Petrescu et al., 2015). In general, drainage results in a decrease in CH_4 emissions from the peat surface (Alm et al., 1999a, 2007; Petrescu et al., 2015), but may increase CH_4 emissions from ditches (Minkkinen and Laine, 2006). The change in climate forcing of C dynamics, caused by drainage for forestry in Finland, is estimated to be negative (cooling) (Minkkinen et al., 2002; Ojanen et al., 2013), but possibly this is balanced out by a decreased albedo effect due to vegetation shifts towards denser coniferous tree cover (Lohila et al., 2010).

1.3 PEATLAND C BALANCE THROUGH TIME

Northern Europe has undergone various climate phases during the Holocene. Between the start of the Holocene, c. 11.7 ka BP, and 9 ka BP (ka = thousand years; BP = before present; present = 1950 AD), summer temperatures were several degrees warmer than today (Väliranta et al. 2015). However, the moisture balance probably resembled present conditions (Nichols et al., 2009; Siitonen et al., 2011). From 9 ka BP, annual temperatures in northern Europe increased, and the period between c. 8 ka and 4 ka BP is called the "Holocene Thermal Maximum" (HTM) (Renssen et al., 2009, 2012; Seppä et al., 2009). In Fennoscandia, the warmest period was between 8 - 6 ka BP, with annual temperatures 2.0 - 2.5 °C higher than pre-industrial times (Davis et al., 2003; Renssen et al., 2009, 2012; Seppä et al., 2009; Mauri et al., 2015). The HTM was also drier than the early Holocene (Korhola et al. 2005; Väliranta et al., 2005; Antonsson et al., 2006; Nichols et al., 2009; Mauri et al., 2015). After the HTM, from c. 4 ka BP onwards, moisture levels increased and annual and summer temperatures gradually decreased towards pre-industrial levels (Nichols et al., 2009; Renssen et al., 2012), although warm and dry anomalies occurred in Fennoscandia between 3 and 0.5 ka BP (Helama et al., 2002; Seppä et al., 2009; Hanhijärvi et al., 2013; Mauri et al., 2015; Wilson et al., 2016), including the warm "Medieval Climate Anomaly" between 1 and 0.5 ka BP (Diaz et al., 2011). Contrasting cold anomalies occurred between 3.8 and 3 ka BP and between 0.5 and 0.1 ka BP (Seppä et al., 2009; Wilson et al., 2016). The latter cold period corresponds to the "Little Ice Age". Finally, temperatures have rapidly increased in northern Fennoscandia since pre-industrial times by up to 2°C, associated with anthropogenic forcing (Mikkonen et al., 2015).

To understand future peatland C dynamics and their expected climate forcing, we have to understand the development of the peatland C reservoir and peat-atmosphere fluxes of greenhouse gases in relation to climate variation in the past. The Holocene is an interesting period because it encompasses the vast majority of the developmental history of northern peatlands (Yu, 2011). The effect of climate conditions during the HTM are of special interest with regard to future climate conditions. Future temperatures are expected to increase more in the high-latitudes than the mid-latitudes and are expected to reach levels similar to those during the HTM (IPCC, 2013). Predictions of future precipitation patterns are relatively uncertain because of the largely regional nature of precipitation (IPCC, 2013), although the frequency and length of extreme dry spells are predicted to increase in northern Europe (Fischer and Knutti, 2014).

Peatlands have played a significant role in the global C balance throughout the Holocene. Peatlands have rapidly spread all over the northern high latitudes after the start of the Holocene (MacDonald et al., 2006; Yu, 2011) and peatland initiation peaked around 11 - 9 ka BP (Yu et al., 2010; Ruppel et al., 2013). Northern peatlands have consistently been a C sink during the Holocene. However, they accumulated C more rapidly in the early Holocene, peaking around 9 - 8 ka BP, compared to the mid- and late Holocene (Yu et al., 2010). Accumulation of C in peatlands seems to have contributed to decreasing atmospheric CO_2 concentrations between 11 and 7 ka BP (Flückiger et al., 2002; Yu, 2011). Since 8-7 ka BP, the average C accumulation in northern peatlands has slowly decreased and the influence on atmospheric CO_2 concentrations has diminished (Yu, 2011).

The magnitude of CH_4 emissions from peatlands are for a large part controlled by total peatland area (Yu et al., 2010, 2013). Therefore, the rapid spread of peatlands in the early Holocene resulted in a rise in atmospheric CH_4 concentrations (Brook et al., 2000; Yu, 2011; Yu et al., 2013). In high latitudes, the initiation of new peatlands and lateral growth of existing peatlands decreased during the HTM (Ruppel et al., 2013) and tropical peatlands became more important in the global CH_4 budget (Brook et al., 2000; Yu et al., 2010), as a consequence of a rapid expansion of tropical peatlands between 8 and 4 ka BP (Yu, 2011). After the HTM, expansion of northern peatlands increased again, probably in response to increased moisture levels linked to decreasing temperatures (Korhola et al., 2010). This period of intensive peat expansion between the end of the HTM and 3 ka BP was also reflected in elevated atmospheric CH_4 concentrations as speculated by Korhola et al. (2010). From 3 ka BP onwards, peatland expansion seems to have decreased probably as most of the suitable area for peat formation was already covered by peat, although this decrease might also have been due to a sampling bias against younger peatlands (Ruppel et al., 2013). In general, the variation in atmospheric CH_4 concentrations seems to follow the global Holocene pattern of peatland expansion (Korhola et al., 2010), although there are some indications that the sources of late Holocene atmospheric CH_4 were at least partly non-natural (Ruddiman, 2007; Yu, 2011).

Although research on peatland development in terms of vegetation succession and C dynamics during the Holocene has been ongoing for several decades, the majority of this work has focused on bogs (Charman et al., 2013 and references therein; Loisel et al., 2014 and references therein). Important exceptions are fen studies by Mäkilä et al. (2001), Mäkilä and Moisanen (2007) and Juutinen et al. (2013) in Fennoscandia, and by Yu (2006), Yu et al. (2003) and Jones and Yu (2010) for North American fens. In general, however, fens have been overlooked and this hinders the establishment of a complete overview of peatland - climate feedback effects. The relative absence of fen studies is undesirable, because fens account for a major proportion of peatlands in subarctic regions where climate warming is predicted to be most severe (IPCC, 2013). Furthermore, northern fens are responsible for the highest CH_4 emissions among peatland types (e.g. Moore and Knowles, 1989; Nykänen et al., 1998; Lai, 2009; Saarnio et al., 2009), and thus increasing our understanding of fen C dynamics under a changing climate is essential.

1.4 PEATLANDS AS ARCHIVES OF ENVIRONMENTAL CHANGE AND CARBON DYNAMICS

Peat accumulates over time and peat layers form an archive, which reflects local environmental conditions at the time of deposition. One method to reconstruct past local habitat conditions is to analyse macroscopic plant remains (plant macrofossils) (e.g. Barber et al., 1998; Mauquoy et al., 2002; Tuittila et al., 2007; Väliranta et al., 2007). The macrofossil analysis is based on species-level identification of plant remains that represent *in situ* deposition (e.g. Mauquoy et al., 2002). Reconstructed peatland plant assemblages are proven to be a good proxy to quantitatively reconstruct water level changes (e.g. Väliranta et al., 2007, 2011) and can also be used to infer changes in nutrient status (e.g. Tuittila et al. 2013) and temperature (e.g. Kultti et al., 2004). In addition, testate amoebae, which are a microbial group of protists, can be used to reconstruct past hydrological conditions (Charman and Warner, 1997) and biomarkers from organic matter can be used to reconstruct changes in peatland vegetation (e.g. Ronkainen et al., 2014). Pollen assemblages can be used to reconstruct more regional-scale environmental changes (Cain, 1939).

The dynamics of C accumulation can be reconstructed by measuring the C content and peat age throughout peat profiles. To date, relatively few studies have incorporated lateral expansion in Holocene-scale peatland development reconstructions (Korhola, 1994; Mäkilä, 1997; Bauer et al., 2003; Mäkilä and Moisanen, 2007), and even fewer studies have applied a three-dimensional approach to reconstruct peatland C dynamics (Korhola et al., 1995, 1996). The long term uptake of atmospheric CO_2 can be derived from the C accumulation rate (Frolking and Roulet, 2007). The C lost from the peatland as dissolved organic carbon (DOC) is not taken into account in estimating CO_2 uptake, with the assumption that most of the DOC rapidly mineralizes to CO_2 and returns to the atmosphere (e.g. Köhler et al., 2002).

Peatland CH_4 fluxes are regulated by multiple factors, such as water level, nutrient level, temperature, plant species composition and productivity (Moore and Knowles, 1989; Bellisario et al., 1999; Walter and Heimann, 2000; Joabsson and Christensen, 2001; Leppälä et al., 2011). However, several studies have shown that vegetation composition can be used as a proxy for CH_4 fluxes (Bubier et al., 1995; Dias et al., 2010; Couwenberg et al., 2011; Audet et al., 2013; Gray et al., 2013). Consequently, fossil plant assemblages can be used to reconstruct past CH_4 fluxes.

Reconstructed C dynamics, CO_2 and CH_4 fluxes, can be used to assess the impact of peatlands on climate throughout their development history. This impact on climate, expressed as radiative forcing (RF) (Myhre et al., 2013), can be modelled by evaluating the effect of sustained CH_4 emissions and CO_2 uptake on atmospheric concentrations (Frolking et al., 2006). When assessing climate effects it is essential to take into account the differences in the radiative efficiency and the atmospheric lifetimes of CO_2 and CH_4: although the radiative efficiency per molecule of CH_4 is c. 26 times that of CO_2 (Forster et al., 2007; Frolking and Roulet, 2007), the lifetime of the emitted CH_4 is in the order of decades compared to an adjustment time of many millennia for CO_2 (Forster et al., 2007; Frolking and Roulet, 2007). The radiative efficiencies of CO_2 and CH_4 vary depending on background atmospheric concentrations, and variation during the study period should be incorporated in radiative forcing modelling (Lohila et al., 2010). The more traditional way of expressing climate impact has been the Global Warming Potential (GWP) approach (e.g. Roulet, 2000; Whiting and Chanton, 2001). However, GWP assesses the RF of an instantaneous pulse of greenhouse gases on atmospheric concentrations and does not evaluate the impact of sustained gas emissions and uptake or the dynamics of C fluxes over time (Frolking et al., 2006). Furthermore, GWP ignores variations in background concentrations. Thus, the GWP concept is not suitable to assess the climate impacts of long-term peatland development.

1.5 RESEARCH AIMS AND APPROACH

The aim of my thesis project was to investigate Holocene peatland development and associated changes in vegetation composition, C accumulation and CH_4 emission patterns in three Finnish peatlands. These peatlands represent different types of northern peatlands; a meso-eutrophic fen, an oligotrophic fen-ombrotrophic bog peatland complex and an ombrotrophic bog managed for forestry. All collected palaeoecological data were used to create a set of radiative forcing reconstructions. Special attention was paid to the Holocene Thermal Maximum period, which I assumed as a potential analogue for the future. My research hypotheses were:

1. The warm and dry conditions during the HTM resulted in a decrease in C accumulation and lateral expansion rates.
2. C accumulation rates also reflect the successional stage of peatlands.
3. Long-term atmospheric RF, calculated from reconstructed peatland C dynamics, can be used to explore climate-peatland feedback mechanisms.

The study sites consisted of a sub-arctic meso-eutrophic fen (**I**), a southern boreal peat complex containing oligotrophic (poor) fen and bog areas (**II**), and a southern boreal ombrotrophic bog drained for forestry in 1969 (**III**). To simplify the communication of variability between the study sites in this thesis, I use the term 'peatland type' to refer to these differences in nutrient level, floristic characteristics, etc. Based on this reasoning the peatland types encountered in this study are meso-eutrophic fen, oligotrophic fen, ombrotrophic bog and drained ombrotrophic bog. The age of the bottom peat layer was analysed at multiple points in each site in order to reconstruct the lateral expansion of the peatland during the Holocene (**I**, **II**, **III**). Further long core age analyses were made for one (**I**), two (**II**), and five (**III**) peat cores, in order to reconstruct vertical peat growth over time. Carbon accumulation rate (CAR) values over time were calculated for one (**I**), two (**II**), and eight (**III**) peat cores. The vegetation at the study sites was reconstructed by analysing the plant macrofossils in peat samples of various depth and age (**I**, **II**, **III**). CH_4 emissions were reconstructed based on contemporary CH_4 flux measurements and reconstructed vegetation composition (**I**, **II**, **III**), using a transfer function of plant macrofossils (**II**), or with the addition of mire site type specific emission rates from literature (**III**). The development of peatland RF was calculated on the basis of reconstructed CAR and CH_4 emission rates multiplied by the reconstructed peatland area (**I**, **III**). The RF of the subarctic rich fen (**I**) was recalculated for this synthesis using a slightly altered methodology and the RF of the peat complex (**II**) was not included in the article, but was calculated later for this synthesis. The reason for the re-calculation of the RF of site **I** is discussed in Section 3.6. Finally the resulting reconstructions of peatland lateral expansion, CAR, vegetation and RF were compared to Fennoscandian climate reconstructions to evaluate how the study sites responded to changing climate (**I**, **II**, **III**).

2 STUDY SITES

The three study sites (Fig. 1) were selected to cover the different peatland development pathways that can be found in Finland. The sites are: a subarctic fen, Lompolojänkkä, which has remained meso-eutrophic throughout its development; a boreal peatland, Siikaneva, which is a peatland complex and has partly transformed into an ombrotrophic bog; and a boreal forested peatland, Kalevansuo, which was an ombrotrophic pine bog before drainage for forestry. These sites were chosen because of ongoing research on contemporary C dynamics (Lompolojänkkä: Aurela et al., 2009, 2015; Drewer et al., 2010; Pearson et al., 2015; Siikaneva: Aurela et al., 2007; Rinne et al., 2007; Riutta et al., 2007; Laine et al., 2012; Kalevansuo: Pihlatie et al., 2010; Badorek et al., 2011; Lohila et al., 2011; Ojanen et al., 2012; Koskinen et al., 2014).

2.1 SUBARCTIC FEN, LOMPOLOJÄNKKÄ

Lompolojänkkä (68.0°N, 24.2°E, 269 m a.s.l.) (**I**) is located in the sub-arctic aapa mire region in north-western Finland. Aapa mires are characterized as minerotrophic wet mires, often having a pronounced surface pattern of wet flarks separated by parallel hummocky strings (Eurola et al., 1984). However, Lompolojänkkä fen, which is located in a small valley bordered by gentle slopes, lacks this patterning and has a uniform surface microtopography. It is an open, nutrient-rich sedge fen where the

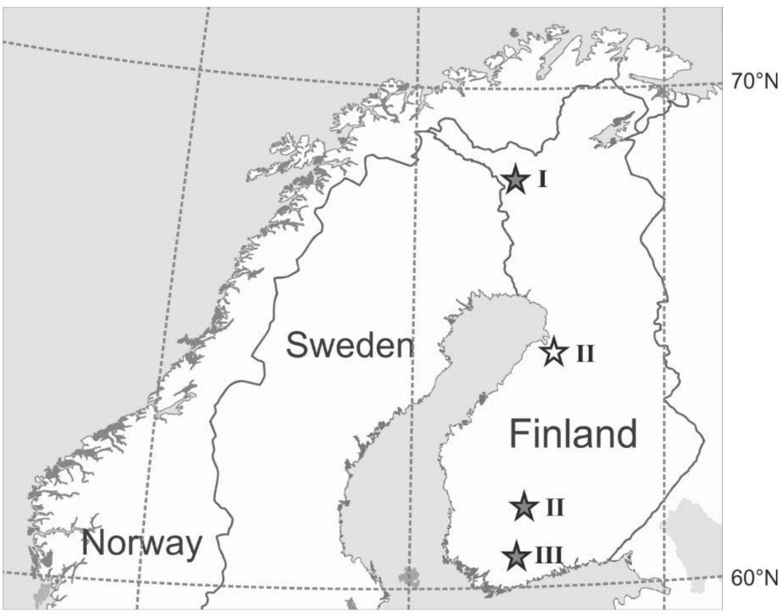

Figure 1. Location of the study sites. Lompolojänkkä (I), Siikaneva (II) (filled star symbol) and Kalevansuo (III). The open star indicates the location of a supplementary study site Siikajoki.

vegetation is dominated by *Carex* spp., *Betula nana*, *Menyanthes trifoliata* and *Salix lapponum*. The moss layer is patchy and mainly consists of minerotrophic peat mosses, such as *Sphagnum fallax*. Willow bushes (*S. lapponum*) fringe a small stream that runs through the fen. The peat layer is up to 2.5 m thick and currently spans an area of c. 14 ha.

2.2 PEATLAND COMPLEX, SIIKANEVA

The studied peatland complex, Siikaneva **(II)**, is located in the southern boreal region of Finland, 61°50'N, 24°12'E, 160 m a.s.l. Siikaneva is an open peatland that has bog and fen areas. Large oligotrophic small sedge fens form the majority of the total area of c. 12 km^2. Peat depth ranges from 2 to 6 m. Most of the fen surface has a relatively uniform lawn topography, with the vegetation consisting of a moss layer (*S. balticum*, *S. majus* and *S. papillosum*) and a sparse vascular plant layer dominated by Cyperaceae species (*Eriophorum vaginatum*, *Carex rostrata* and *C. limosa*). The bog areas have a distinctive microtopographical pattern with hummocks, dominated by *S. fuscum* and *S. rubellum*, lawns with mostly *S. magellanicum* and *S. rubellum*, wet hollows dominated by *S. cuspidatum* and *S. majus*, and ponds and bare peat surfaces without a moss layer. Dwarf shrubs, such as *Andromeda polifolia*, *Calluna vulgaris* and *Empetrum nigrum*, are present on the hummocks. *E. vaginatum* grows on the dry lawns and encroaches onto the hummocks. *Rhynchosphora alba*, *Carex limosa* and *Scheuchzeria palustris* occur in wet hollows and border the bare peat surfaces.

2.3 DRAINED OMBROTROPHIC BOG, KALEVANSUO

Study site Kalevansuo (**III)** is also located in the southern boreal region (60°38'49"N, 24°21'23"E; elevation 123 m a.s.l.). The pre-drainage vegetation represented a nutrient poor dwarf-shrub pine bog, but after drainage in 1969 the growth of the tree stand increased. The tree stand is dominated by *Pinus sylvestris*, with the occasional *Betula pubescens* and understory *Picea abies*. Dwarf shrubs consist of *Ledum palustre*, *Vaccinium uliginosum*, *V. vitis-idaea*, *V. myrtillus*, *E. nigrum* and *C. vulgaris*. *E. vaginatum* and *Rubus chamaemorus* occur in the field layer. The moss layer consists of forest mosses (*Pleurozium schreberi*, *Dicranum polysetum*, *Aulacomnium palustre*, *Polytrichum strictum*). Moist patches support peat mosses such as *S. angustifolium*, *S. magellanicum* and *S. russowii*. The size of Kalevansuo is c. 90 ha and the peat depth ranges from 0.4 to 3 m (Lohila et al., 2011).

3 METHODS

3.1 PEAT CORING

Peat cores were collected from the three sites to study both the vertical growth and lateral expansion. A differentiation was made between the peat cores used to study vertical growth, which covered the entire peat depth, and the additional cores used to study lateral expansion, which were sampled from the bottom-most peat layer. The peat cores covering the entire peat depth are hereafter referred to as 'long cores' and the peat samples from peat layers just above the substrate are hereafter referred to as 'basal samples'. The coring locations were spread over the whole peatland. All long cores were collected from intermediate lawn surfaces, because these habitats are most sensitive to changing hydrological conditions and thus likely to reflect variations in environmental conditions. The following number of cores were sampled for this study: 1 long core and 8 basal samples from Lompolojänkkä (**I**), 2 long cores and 16 basal samples from Siikaneva (**II**), and 8 long cores and 11 basal samples from Kalevansuo (**III**).The study sites were sampled in 2010 (**I** and **II**) and 2012 (**II** and **III**), using a Russian peat corer with a 5-cm diameter cylinder.

3.2 CHRONOLOGY

Peat samples were sent for Accelerator Mass Spectrometry ^{14}C dating to the Finnish Museum of Natural History (LUOMUS) (former Dating Laboratory) or to the Poznan Radiocarbon Laboratory in Poland. All peat basin samples and multiple samples from the long cores were dated, with particular focus on where the peat characteristics changed. A total of 77 peat samples were dated. The obtained radiocarbon ages were calibrated using IntCal09 (Reimer et al., 2009) (**I**) and IntCal13 (Reimer et al., 2013) (**II** and **III**). The calibrated two-sigma median age was used as an age estimation, expressed as calibrated years before present (cal. BP). Age-depth models were constructed for long cores with multiple dates using the 'BACON' software (Blaauw and Christen, 2011). These age-depth models provided weighted average mean ages (cal. BP) over the whole peat profile, which were used to estimate the age of any peat layer that was not radiocarbon dated.

3.3 VEGETATION RECONSTRUCTION

The vegetation of the peatlands was reconstructed by analysing the macrofossil plant remains throughout the long cores (**I**, **II** and **III**). The long cores were horizontally sliced into 2-cm thick slices. Plant macrofossils were analysed in slices taken every 4 cm (**I**), 20 cm (**II**), or 8 cm (**III**) depth. The plant macrofossil analysis followed the Quadrat and Leaf Count protocol described by Mauquoy and Van Geel (2007) and modified by Väliranta et al. (2007). Volumetric sub-samples of 5 cm^3 were taken from the long core slices and cleaned under running water using a 140-μm sieve. The material remaining on the sieve was first examined under a low power stereomicroscope. Volumetric percentages were determined for different plant types, e.g. *Sphagnum*, other bryophytes, *Eriophorum vaginatum*, Cyperaceae, and Ericaceae. If the proportion of mosses exceeded 10%, a high-power light microscope was used for species level identification. Charcoal particles were also counted during macrofossil analysis (**II** and **III**) to investigate the occurrence of peat fires.

3.4 LATERAL EXPANSION

The dated basal peat samples were used to reconstruct where peat initiation first occurred and how the peatland area expanded afterwards. The extent of the peatland area of Lompolojänkkä throughout the Holocene was reconstructed based on the modelled distribution basal age (**I**). Siikaneva and Kalevansuo were too large, and too irregular in shape for this approach. For these study sites, the basal peat age was manually estimated within 1000 to 3000 year time windows throughout the Holocene, using the basal dates and information on substrate topography (**II**, **III**).

3.5 CARBON ACCUMULATION

Peat bulk density (BD) and organic matter content were analysed for alternating slices of all long cores (**I**, **II**, **III**). Organic matter content was measured by quantifying the mass loss after heating the peat to 550 °C for 2 hours (Chambers et al., 2011). The difference in dry mass before and after heating constitutes the organic matter content percentage, or loss on ignition (% LOI). The C content of the peat (expressed as % of organic matter) was determined for one peat core from Kalevansuo (**III**). In studies **I** and **II,** the average organic matter C content was assumed from literature values (Loisel et al., 2014). The C content was multiplied by LOI and BD to calculate the amount of C in each peat slice. This was then combined with the calibrated ages of the peat slices to calculate the apparent CAR (g C m^{-2} a^{-1}) for all long cores throughout the Holocene (**I**, **II**, **III**).

In addition, BD was analysed for all 18 peat cores from Siikaneva (**II**). For those 16 cores where LOI was not measured it was assumed to be similar to the average LOI from the two long cores and these values were used to calculate CAR for the entire peatland over the Holocene.

3.6 PEATLAND CARBON DYNAMICS

To analyse the peatland-climate feedback, I calculated the peatland RF resulting from the exchange of C between the peatland and the atmosphere. Here I followed the micrometeorological sign convention for CO_2 and CH_4 fluxes: a positive sign indicates a flux from the ecosystem to the atmosphere (emission) and a negative sign indicates a flux into the ecosystem (uptake). The reconstructed CO_2 and CH_4 fluxes were calculated for the long cores. They were averaged for each study site and multiplied by the peatland area to calculate the peatland scale fluxes throughout the Holocene. The contemporary CO_2 and CH_4 fluxes between peatland and atmosphere were used to calculate the development of RF of each study site throughout the Holocene.

3.6.1 CO_2 UPTAKE

In this study, the CAR values of the respective study sites were used as net CO_2 uptake rates (g C m^{-2} a^{-1} = g CO_2-C m^{-2} a^{-1}) throughout the Holocene (**III**) (cf. Walter Anthony et al., 2014). However, in Lompolojänkkä (**I),** I applied a different method to estimate Holocene CO_2 uptake rates. In **I,** the estimated CH_4-C emissions were added to the CO_2-C uptake by the peatland, with the assumption that the emitted CH_4 originated from CO_2 that was taken up by plants growing on the peatland. However, CH_4 emitted to the atmosphere by the peatland is rapidly oxidised to CO_2 (Ramaswamy et al., 2001). Thus the fraction of CO_2-C uptake that was emitted as CH_4-C can be neglected, because it had only left the pool of atmospheric CO_2 for a period in the range of decades (Frolking et al., 2006). Therefore, I retrospectively concluded that the method introduced in publication **I** had incorporated an incorrect assumption and that the CO_2-C uptake was an overestimation. The reconstruction of CO_2 uptake in Lompolojänkkä and the RF were recalculated based on the method applied in article **III** and the results of the corrected RF are given in this thesis.

3.6.2 CH_4 EMISSION

Methane emissions throughout the Holocene were estimated using information on past vegetation composition and contemporary CH_4 flux values measured in the study sites. Two different methods were applied: using average CH_4 flux values corresponding to different peatland types (**I** and **III**); and by establishing the relationship between plant species and CH_4 flux to predict the CH_4 flux in the past (**II**).

In Lompolojänkkä and Kalevansuo, plant macrofossil data from the long cores were used to describe the peat type or successional stage of the peatland at different times during the Holocene. The contemporary CH_4 fluxes measured on peatlands were assumed to be analogous to past fluxes. In Lompolojänkkä, the plant macrofossils suggested that the peatland has been a meso-eutrophic fen throughout its history (**I**). Consequently, the CH_4 flux was assumed to have been constant at the level that was measured in Lompolojänkkä between 2005 and 2010: *viz.* 15.2 g CH_4-C m^{-2} a^{-1} (Aurela et al., 2009; unpublished data). However, to account for uncertainties in estimating past CH_4 fluxes, I developed additional scenarios of past CH_4 flux. In these additional scenarios the past CH_4 flux corresponded to (a) the maximum CH_4 emissions measured in Finnish fens; 30 g CH_4-C m^{-2} a^{-1} (Huttunen et al., 2003; Saarnio et al., 2007), (b) no CH_4 emissions; 0 g CH_4-C m^{-2} a^{-1}, representing an extreme lower limit, and (c) the contemporary CH_4 flux at Lompolojänkkä; 15.2 g CH_4-C m^{-2} a^{-1}, but which can be assumed to have decreased to zero during the warm and dry conditions of the HTM based on an experimental study conducted in the site (Pearson et al., 2015; see also Nykänen et al., 1998).

In Siikaneva (**II**), the past CH_4 flux was estimated by modelling the plant species - CH_4 flux relationship. This method requires detailed information on plant species composition and CH_4 flux rates, and translates that to an estimation of past CH_4 flux based on the composition of the plant macrofossil record. To reconstruct CH_4 fluxes for both early and later successional stages, data from Siikaneva and a successional series of five young Finnish mires were combined. These young mires are located c. 350 km north of Siikaneva, in the Siikajoki region in central western Finland (Tuittila et al., 2013) (Fig. 1). This combined data consisted of data on vegetation composition and CH_4 flux values from multiple plots in each peatland (61 plots in total). Firstly, the relationship between vegetation composition and the CH_4 flux was established using Canonical Correspondence Analysis (CCA). CCA was performed with CH_4 flux as a constraining variable and Monte Carlo permutation tests (999 permutations) were used to test the significance of the constrained CCA axis (Bubier et al., 1995). Based on the CCA results, predictive models of CH_4 flux using vegetation composition as input were developed using the weighted averaging (WA) method (Ter

Braak and Juggins, 1993). The WA models were then run using the macrofossil assemblages of the long cores from Siikaneva as input. Separate WA models were used for the early successional stages (first 2500 ka after peat initiation, corresponding to mesotrophic fen stage) and later stages. The output of the models was an estimation of past CH_4 emission for each sample in the macrofossil record.

The macrofossil records of Kalevansuo (**III**) show four different successional stages. The contemporary measured CH_4 fluxes for different successional stages, measured on the study site and in other peatlands in Finland, were used to estimate the past flux at Kalevansuo. The different flux values used in Kalevansuo were: 11.2 g CH_4-C m^{-2} a^{-1} for the eutrophic fen; 18.0 g CH_4-C m^{-2} a^{-1} for the oligotrophic fen; 3.7 g CH_4-C m^{-2} a^{-1} for the ombrotrophic bog (Minkkinen and Ojanen, 2013 and references therein); and -0.09 g CH_4-C m^{-2} a^{-1} for the drained bog stage, which is the contemporary flux in Kalevansuo (Lohila et al., 2011).

3.7 RADIATIVE FORCING MODELLING

The reconstructed peatland-scale CO_2 and CH_4 fluxes of the three study sites were used to determine the effect of peatland development on the energy balance of the earth-atmosphere system throughout the Holocene. A sustained pulse-response model was used to calculate the RF that results from the changes in atmospheric concentrations of CO_2 and CH_4, which were caused by CO_2 uptake and CH_4 emissions in the study sites. The used model is similar to the REFUGE model (Sinisalo, 1998; Monni et al., 2003) and has been described in detail by Lohila et al. (2010). In this model, the RF response is related to the decay of a series of annual concentration pulses integrated over a period of time, taking into account the different radiative efficiencies and atmospheric residence times of CO_2 and CH_4 (Table 1), as well as the variation in annual surface fluxes. A similar approach was applied previously by Frolking et al. (2006), Frolking and Roulet (2007), Walter Anthony et al. (2014) and Petrescu et al. (2015). To each of the scenarios in article **I,** a variant (denoted by 'b') was added, in which a DOC sink of 10 g C m^{-2} a^{-1} was assumed (Sallantaus, 1994). This was done to assess the potential effect on RF of the C that does not return to the atmosphere immediately after leaving the peatland as DOC.

Table 1. Summary of C flux parameters used in the atmospheric radiative forcing (RF) model (Forster et al. 2007).

Gas flux (g C a^{-1})	Radiative efficiency (W m^{-2} ppb^{-1})	Lifetime (years)
CO_2	1.4×10^{-5}	> 3000 [a]
CH_4	3.7×10^{-4}	12

[a] A modelled pulse of CO_2 describes a decay response for 3000 years, after which c. 22% of the original pulse is still present and equilibrium is reached.

4 RESULTS AND DISCUSSION

4.1 CHRONOLOGY AND PEAT ACCUMULATION RATES

In total, 77 radiocarbon age analyses were performed: 18 from Lompolojänkkä (**I**), 30 from Siikaneva (**II**) and 29 from Kalevansuo (**III**). The oldest ages indicated that the studied peatlands initiated during the early Holocene peat initiation peak (MacDonald et al., 2006; Yu et al., 2010) at c. 10 ka BP (**I**), 11 ka BP (**II**), and 10.5 ka BP (**III**), respectively. This peak was a result of land availability following deglaciation (MacDonald et al., 2006; Yu et al., 2010) combined with warm and moist conditions (Nichols et al., 2009; Siitonen et al., 2011). The chronologies of vertical peat development were based on long cores with multiple dates, consisting of: 1 core with 10 dates from Lompolojänkkä; 2 cores with 8 and 6 dates from Siikaneva; 5 cores with 5, 3 or 2 dates from Kalevansuo.

The age-depth model of Lompolojänkkä showed a remarkably strong decrease in peat accumulation at c. 8 ka BP (**I**: Fig. 4), coinciding with the maximum warm and dry conditions during the HTM. This pattern had already become apparent when only seven dates were available, but three supplementary radiocarbon analyses were implemented in order to increase the reliability of the chronology. These additional dates all confirmed the presence of a period with strongly reduced peat accumulation rates (**I**: Table 1). The reduction of peat accumulation probably resulted from drying of the peatland (Dorrepaal et al., 2009). Similar decreases in fen peat accumulation rates during past dry periods have been observed in western Siberia (Borren et al., 2004), Alaska (Jones et al., 2009), western continental Canada (Robinson, 2006; Yu, 2006) and in Finland (Mäkilä et al., 2001; Mäkilä and Moisander, 2007).

4.2 VARIATIONS IN VEGETATION COMPOSITION

The macrofossil analysis of Lompolojänkkä (**I**) revealed that it has remained as a meso-eutrophic fen, with vegetation similar to today, throughout its history from 10 ka BP to the present (Fig. 2). The peat was highly humified throughout, but the identifiable macrofossils showed a dominance of sedges (*Carex* spp.) together with other typical eutrophic fen species (e.g. *Paludella squarrosa* and *Sphagnum teres*).

The vegetation composition was reconstructed from two long cores from Siikaneva (**II**). The macrofossils from these cores showed different successional development, as they were collected from a bog and fen area, respectively. The initial vegetation of both sites represented a mesotrophic fen, dominated by sedges and *Equisetum* sp. (Fig. 2). After 1-1.5 ka since initiation of peat accumulation, both locations were transformed into an oligotrophic fen, characterised by the dominance of *E. vaginatum* macrofossils, and the disappearance of eutrophic species macrofossils. In the fen site, the oligotrophic fen stage continued to the present, but in the bog site ombrotrophication started at c. 4.5 ka BP. The bog stage was mainly characterised by dry hummock vegetation. However, the dry bog stage was interrupted by a wet bog phase, from 2.8 to 1.5 ka BP, with ombrotrophic hollow species. The presence of charcoal particles indicate repeated burning of the peatland from 8.5 to 5.5 ka BP and from 2 to 0.5 ka BP.

The vegetation composition was reconstructed for the eight long cores from Kalevansuo (**III**). Peatland initiation started as a eutrophic fen in all sample locations with a basal age older than 3.5 ka BP, but this stage was absent from the younger parts of the peatland (Fig. 2). The eutrophic fen stage was dominated by sedges, together with eutrophic species such as *S. teres*, *Scorpidium scorpioides* and *M. trifoliata*. However, some sampling locations also contained large amounts of Ericaceous shrub remains and *Betula* sp. wood, indicating that peat formation there started via paludification. The oligotrophic fen stage and subsequent bog stage were present in all sampling locations (Fig. 2). The fen-bog transition was restricted to two time periods: c. 4 ka BP and 1-0.5 ka BP. Analysis of the topmost parts of the long cores showed that the recent drainage of the peatland resulted in a replacement of *Sphagnum* spp. by forest mosses, e.g. *Pleurozium schreberi* and *Dicranum polysetum*, and increased cover of woody species. A large amount of charcoal particles was found in Kalevansuo indicating frequent burning from 8 to 4 ka BP and 1 to 0.5 ka BP.

Currently Siikaneva is a peatland complex where multiple peatland types and habitats are mixed and co-occur: ombrotrophic areas with *Sphagnum* hummocks and hollows, oligotrophic fen areas with *E. vaginatum* and oligotrophic *Sphagnum* fen areas. My data show that in the past Kalevansuo also went through such a phase, when part of the peatland was already an ombrotrophic bog, while in other parts the eutrophic fen stage persisted (Fig. 2; **III**: Fig. 3). Asynchronous ombrotrophication (see also e.g. Glaser et al., 1981) is probably caused by variation in local hydrological conditions, for example when the surface water flow from the surrounding area is greater to some parts of the peatland (Tolonen et al., 1979). My data highlights the fact that macrofossil records from a single peat core should not be assumed to provide a complete and overall view of peatland development.

During the first millennia of the Holocene, succession at the study sites seems to have been affected by warm but adequately moist climatic conditions. The subsequent transition in Siikaneva and Kalevansuo from eutrophic to oligotrophic fen, which occurred between 9.5 and 8 ka BP (**II**, **III**), coincided with the onset of the HTM. The low effective humidity of the HTM (Korhola et al. 2005; Väliranta et al., 2005; Mauri et al., 2015) may have promoted the transition to an oligotrophic fen stage with a dominance of *E. vaginatum*, which thrives under variable and low water table levels (Kummerow et al., 1988).

However, the apparent link between climate and peatland succession seems to become less clear during the second half of the Holocene. The vegetation assemblage reconstructions from Siikaneva (**II**: SiiB) and Kalevansuo (**III**: points A and C) suggest that the bog stage started between 5 and 4 ka BP (Fig. 2). Contemporary changes to wetter conditions have also been reported by Tuittila et al. (2007) and Väliranta et al. (2007) for two other nearby bogs in southern Finland. A shift towards wetter climate conditions around 4.5 ka BP in Finland (Snowball et al., 2004) is suggested by peat initiation data (Korhola, 1995; Korhola et al., 1995), diatom data (Korhola et al., 2000) and pollen data (Seppä et al., 2009). In contrast, a second wave of ombrotrophication in Kalevansuo (**III**) occurred between 1 and 0.5 ka BP, which roughly corresponds to the period of the warm and dry Medieval Climate Anomaly

(Diaz et al., 2011). Macrofossil records from Siikaneva indicate alternating moisture conditions inside the ombrotrophic stage, and a change from hummock to hollow conditions between 2.8 and 1.5 ka BP (**II**). This coincided with a change to wet conditions as reported by Tuittila et al. (2007) and Väliranta et al. (2007). Furthermore, the reconstructed vegetation assemblages in Kalevansuo indicate within-site variation in microtopographical hydrological conditions: a shift from hummock to hollow microtopography between c. 400 and 200 years BP in two sample points, which was not observed elsewhere in the peatland. These findings highlight that a response to changing climate may not be uniform among peatlands or even within a single peatland (cf. Loisel and Yu, 2013b). These discrepancies between locations at relatively close distances make interpretation of climate controls on peatland development a challenge, and these data provide an example of how various factors influence peatlands simultaneously.

A striking feature of the oligotrophic fen stage was the frequent occurrence of charcoal in the peat samples, which indicates that the peat surfaces experienced repeated burning. Extensive burning during the *E. vaginatum* dominated phase has been previously observed, for example in the UK (Hughes et al., 2000) and in Finland (Tuittila et al., 2007). It is likely that, in addition to dry conditions, these fires promoted the persistence of *E. vaginatum* (Tuittila et al., 2007). When the period of frequent burning ended, at approximately 4 ka BP (**II**, **III**), the vegetation switched to *Sphagnum* dominance, which started the ombrotrophic stage. Furthermore, at several instances during the ombrotrophic stage in Siikaneva and Kalevansuo (**II**, **III**), fire disturbance led to a reversal in succession from *Sphagnum* spp. back to *E. vaginatum* dominance. The observed periods of elevated fire frequency (**II**, **III**) correspond with other fire studies reported from Finnish and Estonian peatlands (Pitkänen et al., 1999; Morris et al., 2014). These results suggest that the *E. vaginatum* dominated phase may initially reflect succession and prevailing hydrological conditions, but may be sustained by frequent burning, which again reflects climatic conditions (Kuhry, 1994).

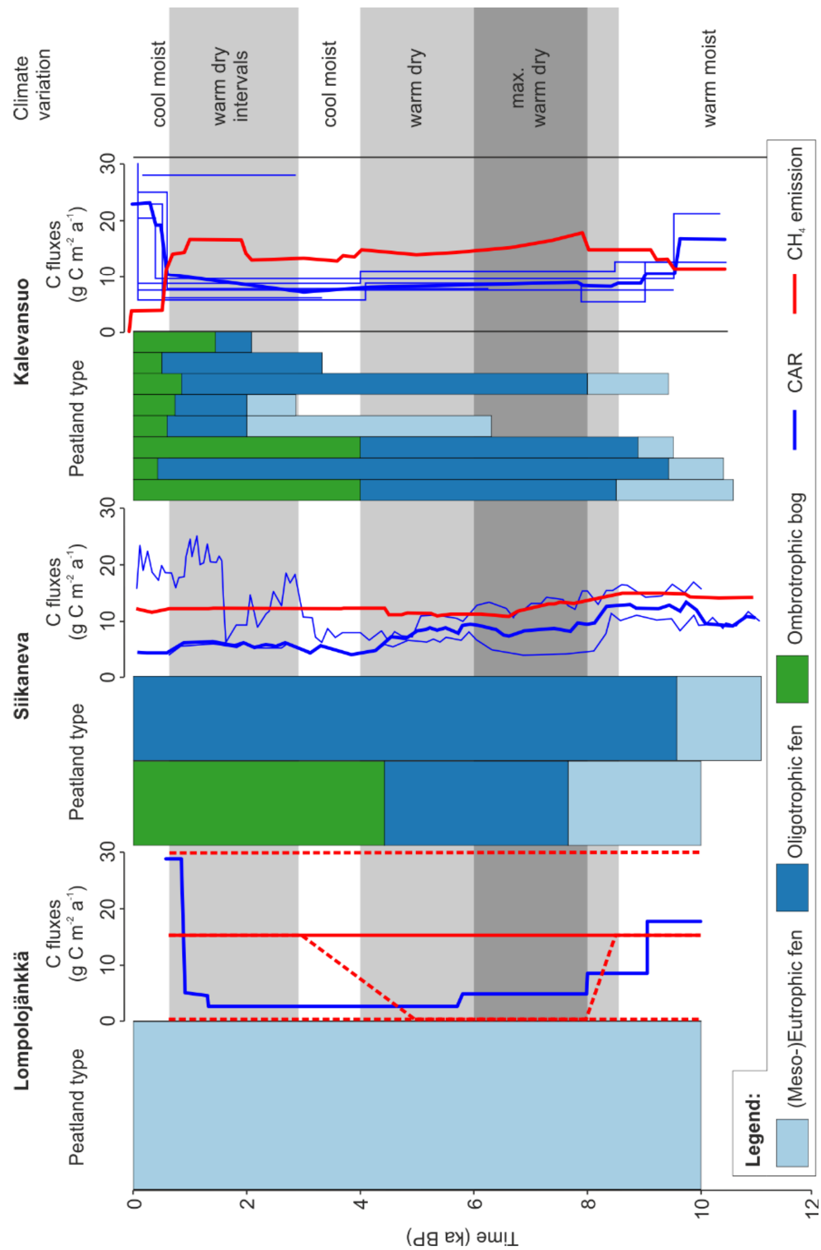

Figure 2. Summary of results from the study sites. Peatland type indicates the reconstructed vegetation assemblage classified as eutrophic fen, oligotrophic fen or ombrotrophic bog. The “peatland type”-columns represent individual long cores. Thin blue lines indicate core-specific carbon accumulation rate (CAR) values and the thick blue line indicates the area-weighted average CAR for each site. The thick red lines indicate the area-weighted average reconstructed methane (CH_4-C) emissions. The dashed red lines in Lompolojänkkä indicate the additional scenarios of CH_4-C emissions.

4.3 LATERAL EXPANSION

During the first thousand years following peat initiation, the peatland area of Lompolojänkkä grew to a tenth of its present area (**I**). Between 9 and 3 ka BP, lateral expansion slowed down and by 3 ka BP the peatland area had reached 36% of the present area. After 3 ka BP, the lateral expansion rate increased with the highest rate estimated for the last thousand years before present. Lateral expansion in Siikaneva (**II**) was fastest between peat initiation at 11 ka BP and 8 ka BP, quadrupling in size every thousand years. After 8 ka BP the lateral expansion rate decreased. For the time period after 5 ka BP, no detailed estimation of lateral expansion could be made, as none of the basal ages were younger than 5 ka BP. Kalevansuo (**III**) expanded rapidly during the first 2.5 ka after peat initiation, between 10.5 and 8 ka BP. After that time lateral expansion continued steadily until 3 ka BP, when rapid expansion occurred towards the north and east.

In general, the fast expansion observed during the first few millennia after peat initiation could be interpreted to reflect the relatively quick infilling of the lowest parts of the basin, before expansion slowed down due to more elevated terrain (Korhola, 1994). However, our basal peat age and peat depth data did not support this theory (**I**: Table 1; **II**: Table 1; **III**: Table 1). In contrast, the reduction in expansion rates, which occurred around 8 - 9 ka BP, seemed to be related to the onset of the HTM. A link between drier climate conditions and decreasing lateral expansion of northern peatlands has previously been observed by Korhola (1994), Mäkilä (1997), Turunen and Turunen (2003) and Ruppel et al. (2013). A second response of lateral expansion to climatic conditions seemed to occur during the late Holocene at c. 3 ka BP. This increase in lateral expansion corresponds with a phase of active lateral expansion reported elsewhere in Northern Europe between 4 and 3 ka BP (Korhola, 1994, 1995; Ruppel et al., 2013). The rapid lateral expansion of the studied sites during the last millennia seems to contradict the suggestion by Korhola et al. (2010) that land surface suitable for peat accumulation was not available by this time. The fact that no increase in the lateral expansion rate was observed in Siikaneva during the last millennia (**II**) could be attributed to the local topography at the edge of the peatland that limits further expansion because of steep slopes (cf. Loisel et al., 2013). A similar relationship between topography and peat expansion was visible in Kalevansuo (**III**) where expansion to the south and west is limited by rising terrain. In conclusion, the lateral peat expansion of the studied sites seems to have been mainly controlled by climatic conditions, but occasionally by topography as well.

4.4 CARBON ACCUMULATION

During the first thousand years in Lompolojänkkä, CAR was c. 17 g C m^{-2} a^{-1} (**I**). From 9 to 5.5 ka BP, CAR slowed down rapidly and remained at c. 2 g C m^{-2} a^{-1} until 1.5 ka BP (Fig. 2). During the last millennia before present, CAR values increased again to c. 30 g C m^{-2} a^{-1}. In Siikaneva (**II**), CAR values showed a clear difference between the bog and the fen sampling locations. CAR values ranged between 6 and 25 g C m^{-2} a^{-1} for the bog location and between 4 and 11 g C m^{-2} a^{-1} for the fen location (Fig. 2). CAR values from both locations decreased between 10 - 4 ka BP, although CAR at the bog site increased again during the bog stage. Similarly, CAR values in Kalevansuo (**III**) decreased after the initial eutrophic fen stage (Fig. 2). CAR values remained low, 5.5 to 10.5 g C m^{-2} a^{-1}, until the second wave of ombrotrophication in Kalevansuo, after which CAR increased to 20 - 25 g C m^{-2} a^{-1} in several locations.

During the HTM, CAR values of the study sites were reduced by 5 to 10 g C m^{-2} a^{-1} (Fig. 2). In some sampling locations this decrease in CAR occurred rapidly (**I**; **II** fen) at the time of the onset of the HTM. In other cases (**II** bog; **III**) the decrease in CAR was more gradual. At three points in Kalevansuo (**III** sampling locations A, B, C) this reduction in CAR was linked to a change in peat type from eutrophic fen to oligotrophic fen, however the decrease in CAR was not associated with a change in peat type in Lompolojänkkä (**I**) and Siikaneva (**II**). The decreased CAR values after 8.5 ka BP are probably an effect of the dry conditions during the HTM, which were less favourable for peat growth than the preceding early Holocene (Yu et al., 2010). Similar evidence of peatland CAR values decreasing during dry conditions has been observed before in Finnish mires (Mäkilä et al., 2001; Mäkilä and Moisanen, 2007), in Siberia (Borren et al., 2004), in Alaska (Jones et al., 2009), in Canada (Robinson, 2006; Yu, 2006) and in collected data from northern peatlands (Yu et al., 2009; Loisel et al., 2014).

A prominent and rapid increase in CAR values from 2000 to 100 years BP was observed in all study sites, although not in all sampling locations (Fig. 2). In Kalevansuo, this increase was linked in some cases to a change in peatland type from oligotrophic fen to *Sphagnum* bog (**III**), while in Siikaneva CAR values increased not at the onset but inside the bog stage (**II**). Higher CAR values can be expected in younger peat layers, because younger peat has had less time to decompose (Clymo, 1984), but the transition in CAR from older to younger peat layers should be more gradual than observed in this study. In both Siikaneva (**II**) and Kalevansuo (**III**) there was evidence of frequent fires occurring during the period of reduced CAR values, which could explain the low CAR values (Kuhry, 1994; Pitkänen et al., 1999) and the subsequent rise in CAR values might reflect less frequent burning.

The pattern of high CAR values during the early Holocene, reduced CAR values during the mid-Holocene and high CAR values during the late Holocene, corresponding to the (meso-)eutrophic fen, oligotrophic fen and bog stages, respectively, has also been observed by Mäkilä (1997), Mäkilä et al. (2001), Mäkilä and Moisanen (2007) and Peteet et al. (2016). Mäkilä (1997) also observed evidence of the effect of frequent fires on low CAR values. The average CAR value for oligotrophic fens in Finland is 17 ± 8 g C m^{-2} a^{-1} (Turunen et al., 2002). The much lower CAR values observed in this study (3 - 10 g C m^{-2} a^{-1}) during the oligotrophic fen stage could be explained by the occurrence of frequent fires. The average CAR value of northern peatlands is 22.9 ± 2.0 g C m^{-2} a^{-1} (Loisel et al., 2014), although these values are not specific for oligotrophic fens but include eutrophic fens and ombrotrophic bogs. The results from my study indicate that climate variation may have a large influence on CAR values. In addition to the large climate impact, they also show that the effect of climate variation on CAR may vary within a peatland because of variation in microtopography (Alm et al., 1997, 1999b; Bubier et al., 2003; Cliche Trudeau et al., 2012; Loisel and Yu, 2013b), sensitivity of peat type (Verhoeven and

Toth, 1995), and small-scale hydrology (Klein et al., 2013). Moreover, fires, regardless if they are related to climatic conditions or not, have an additional major effect on CAR.

It may be that the recent increase in CAR values, in addition to the influence of peatland type (Tolonen and Turunen, 1996; Drewer et al., 2010) and age (Clymo, 1984), is linked to climate changes towards cooler and moister conditions during the 'Little Ice Age' (Diaz et al., 2011; Wilson et al., 2016). However, it remains unclear whether the change in CAR was a direct effect of climate variation or an indirect effect through fire patterns (Kuhry, 1994).

4.5 RADIATIVE FORCING

In Lompolojänkkä (**I**) and Kalevansuo (**III**), CH_4 emissions were reconstructed based on the prevailing peatland type, which was inferred from the vegetation reconstructions (Fig. 2). For Lompolojänkkä, the reconstructed CH_4 flux was equal to the contemporary flux of 15.2 g CH_4-C m^{-2} a^{-1}. In Kalevansuo it ranged from 11.2 to 17.6 g CH_4-C m^{-2} a^{-1} between 10.5 and 1 ka BP. Subsequently, when all parts of Kalevansuo had transitioned into a bog stage, the CH_4 flux decreased to 3.7 g CH_4-C m^{-2} a^{-1} and in the post-drainage period there was a slight uptake of -0.09 g CH_4-C m^{-2} a^{-1}. The WA model of CH_4 flux in Siikaneva, based on the relationship between present-day vegetation and CH_4 flux, gave results similar to the other study sites; from 11 to 15 g CH_4-C m^{-2} a^{-1} (**II**). All three study sites had lower CAR than CH_4-C emissions for the majority of the Holocene (Fig. 2). Consequently, CH_4 emissions played a prominent role in the peatland C balance throughout the Holocene. Model output uncertainties for Siikaneva were large, but the approach for the other two sites did not allow us to consider uncertainties. Therefore, additional CH_4 flux scenarios were added for Lompolojänkkä (Fig. 2) to explore the effect on RF of extreme high, low, or variable past CH_4 fluxes (Fig. 3).

Methane has a larger RF effect compared to CO_2 over short time scales (up to 100 years). However, in contrast to CH_4, the RF of CO_2 is maintained for many thousands of years (Table 1). Consequently, peatlands that simultaneously accumulate C and emit CH_4 will exhibit an initial positive RF (warming the atmosphere) caused by CH_4 emission. This initial stage is followed by a decrease of RF towards negative values (cooling) caused by the long term effects of CO_2 uptake (Frolking et al., 2006). As CH_4 emissions form a major part of the peatland C balance, variation in CH_4 emissions had a large effect on RF and overshadowed the effect of CO_2 uptake over short time scales (Fig. 3) (cf. Frolking et al., 2006). In my study, due to the low CO_2 uptake and relatively high CH_4 emissions, it took thousands of years before the RF became negative (Fig. 3b and c) and in the case of Lompolojänkkä the RF never turned negative (Fig. 3a). Frolking and Roulet (2007) estimated that northern peatlands collectively would have reached a negative RF at the latest 3.5 ka after initiation. However, Siikaneva and Kalevansuo changed to a negative RF mode only after 4.3 and 7 ka since initiation, respectively (Fig. 3b, c), as the long term CO_2 uptake in these sites remained low for extended periods of time, in contrast to Frolking and Roulet (2007) who assumed a constant CO_2 flux per unit area. However, my results are similar to the estimated RF switchover time of Reksuo-bog in southern Finland, c. 6 ka (Korhola et al., 2010), and with the model results of Frolking et al. (2006).

In Lompolojänkkä, the turnover from positive to negative RF only occurred in the 'variable' scenario where CH_4 emissions were decreased to zero at 8 ka BP (Fig. 3). In the scenario with zero CH_4 emissions throughout the peatland history, the RF remained negative. In the other scenarios, i.e. assuming the current level of emissions (15.2 g CH_4-C m^{-2} a^{-1}) and maximum CH_4 emissions (30 g CH_4-C m^{-2} a^{-1}), the RF became increasingly positive until CAR values increased tenfold at c. 1 ka BP (Fig. 2). This sustained increase of RF until 1 ka BP was not the result of an increase in CH_4 emission rates, but reflects the expansion of the peatland area, which continuously leads to an increase in the total annual amount of CH_4 added to the atmosphere. The uptake of CO_2 in Lompolojänkkä was so low, approximately 2 g C m^{-2} a^{-1} between 8 and 2 ka BP (Fig. 2), that the resulting cooling effect was never enough to overcome the warming effect of CH_4 emissions. As a consequence, even though the peat archive suggests that Lompolojänkkä has been a constant C sink during the Holocene (**I**), it seems that this peatland retained a slight climate warming effect even until today; 10 ka since the initiation of peat accumulation.

Drainage of Kalevansuo in 1969 resulted in a significant change in the vegetation composition and C dynamics (**III**). The post-drainage soil CO_2 and CH_4 fluxes were: -65.5 g CO_2-C m^{-2} a^{-1} and -0.09 g CH_4-C m^{-2} a^{-1}, respectively (Lohila et al., 2011; Ojanen et al., 2012). Drainage is visible in the vegetation assemblage reconstructions but not in the CAR values, as the dating and sampling resolutions were not high enough for the top-most peat layers. However, the contemporary C dynamics of Kalevansuo were extrapolated for the post-drainage period RF calculation, and an effect is just visible as a decrease in RF after zero cal. BP (Fig. 3c). Because Kalevansuo has continued to sequester C even after drainage, as a consequence of moderate water level drawdown combined with the production of resilient litter by the post-drainage vegetation (Minkkinen et al., 2002; Laiho, 2006; Lohila et al., 2011), the RF might possibly decrease further for another 50 to 100 years and then gradually return to the RF level before drainage (Laine et al., 1996).

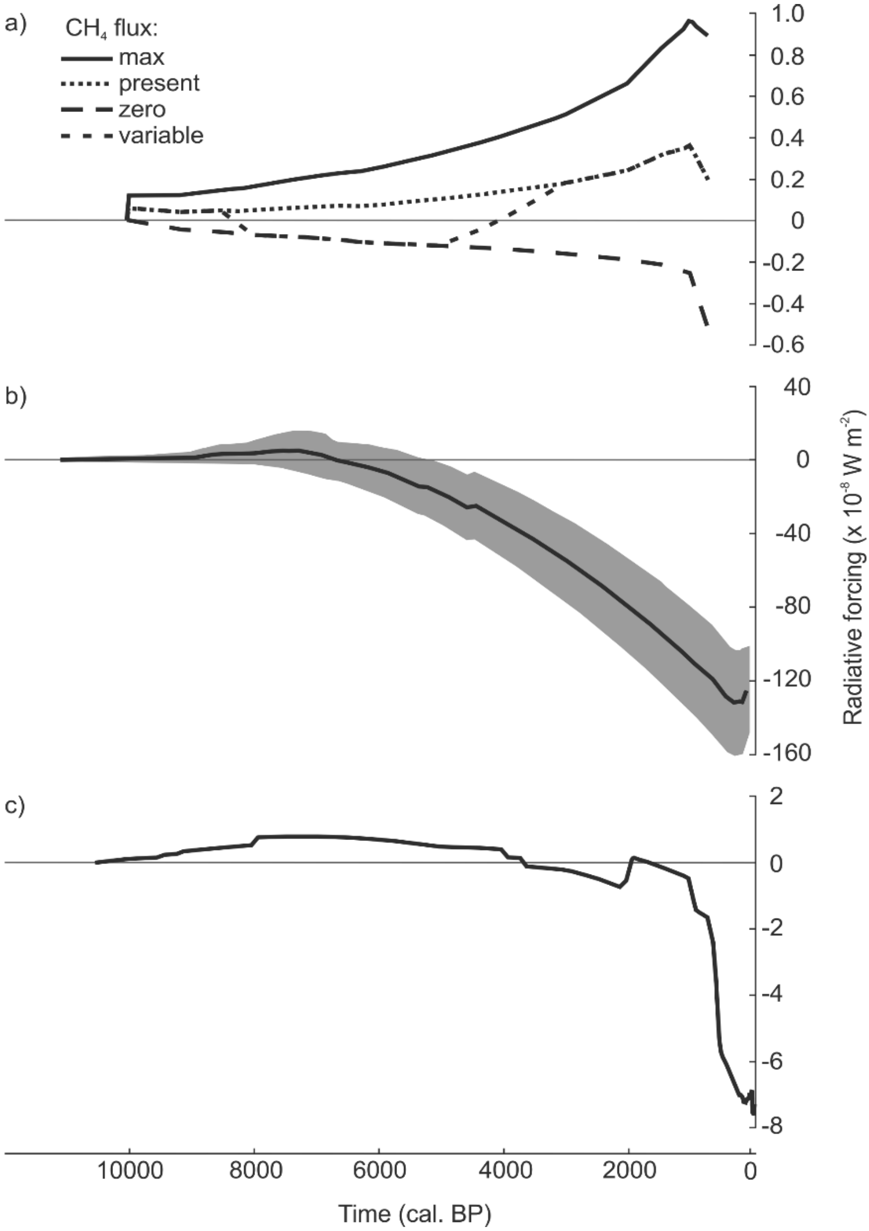

Figure 3. Radiative forcing (x 10^{-8} W m^{-2}) based on the reconstructed carbon dioxide (CO_2) and methane (CH_4) fluxes of a) Lompolojänkkä (**I**), b) Siikaneva (**II**) and c) Kalevansuo (**III**). In a) the different lines represent CH_4 flux scenarios: max = maximum CH_4 emission of 30 g CH_4-C m^{-2} a^{-1}; present = emission equalled contemporary value of 15.2 g CH_4-C m^{-2} a^{-1}; zero = emission did not occur (0 g CH_4-C m^{-2} a^{-1}); variable = emission equalled contemporary value but decreased to zero between 8 and 5 ka BP. These scenarios correspond to scenarios 2a, 1a, 3a and 4a (**I**: Table 2), respectively. In b) the shaded area indicates radiative forcing uncertainty based on the prediction errors of the CH_4 flux reconstruction (**II**).

5 CONCLUSIONS

5.1 MAIN OBSERVATIONS

- Peatland vegetation seemed to respond strongly to peat fires. The results suggest that frequent fires at least partly controlled the transition from fen to bog.

- Based on the ages of the basal peat, the lateral expansion of the three study sites decreased at the onset of the HTM but increased again during the cool and moist period after the HTM. This suggests that the rate of lateral expansion was controlled by changes in climate conditions to a large extent.

- In many cases, CAR values decreased at the onset of the HTM, but they also reflect the successional stage of the peatland. Ombrotrophic stages had higher CAR values than minerotrophic fen stages.

- CAR values were very low in all three study sites. Abundant evidence of peat fires during and after the HTM suggests that frequent fires limited C accumulation during long periods of the Holocene.

- RF at the study sites was positive (warming the atmosphere) for a very long time before it became negative. In the northernmost site, it possibly remained positive until the present. This is a result of very low long term CO_2 uptake and relatively high CH_4 emissions.

- Lateral expansion of the peatlands resulted in a short term increase in RF, because of the different radiative efficiency and temporal scale on which the CH_4 emissions (fast) and CO_2 uptake (slow) affect atmospheric radiation.

- Individual peatlands showed asynchronous development between different parts of the peatland. This is evident both in the successional stages and the CAR values, and highlights the necessity to study multiple peat cores per site before conclusions can be drawn.

5.2 CLIMATE - PEATLAND FEEDBACK LOOPS

My data suggest that peatland succession was linked to fire events (**II**, **III**), which may form a positive feedback loop (Fig. 4). This feedback loop consists of the following components: an increase in fire events caused by dry conditions and frequent extreme dry weather; frequent fire events that promoted the prevalence of *Eriophorum vaginatum* and inhibited ombrotrophication; ombrotrophication that would have increased CO_2 uptake and decreased CH_4 emissions, although this was delayed; and both the low CO_2 uptake and high CH_4 emissions resulted in an additional positive effect on the warm and dry climate conditions.

My study also highlights the importance of the ratio of long term CO_2 uptake versus short term CH_4 emission for the development of RF. Furthermore, my results suggest a possible negative feedback loop (Fig. 4): cool and moist conditions promote lateral peatland expansion; peatland expansion leads to an increase in total CH_4 emissions, because of an increase in fen peat area; over the long term peatland expansion leads to increased total CO_2 uptake; CH_4 has a larger RF in the short term; the rapid increase in CH_4 emissions and its stronger short term effect have a warming effect on the climate. In the long term, this warming effect may be compensated by the increase in total CO_2 uptake.

A third feedback mechanism suggested by my study is a positive feedback loop (Fig. 4): dry conditions resulted in reduced CO_2 uptake (directly or through fires); the decreased CO_2 uptake has a warming effect on the climate.

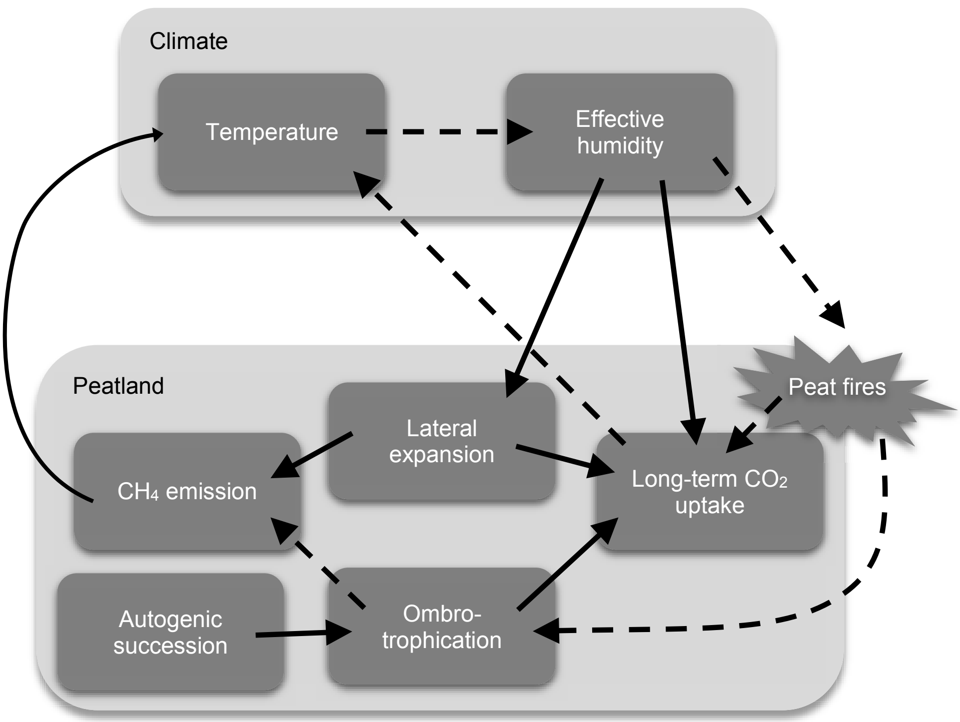

Figure 4. Feedback loops between climate and peatlands suggested by the results of this study. The solid arrows indicate a positive effect and the dashed arrows a negative effect. The assumption is that effective humidity decreases when temperatures rise (i.e. either warm and dry or cool and moist). However, this reflects the situation during the Holocene Thermal Maximum and does not necessarily describe future climate in Fennoscandia (Rowell and Jones, 2006).

5.3 FUTURE PERSPECTIVES

The results of my study indicate that lateral expansion of peatlands does not process linearly. This conclusion is similar to the findings of previous studies (e.g. Korhola, 1994, 1995). However, recent estimations of large scale peatland expansion during the Holocene have been based on data from peatlands with only one (Yu et al., 2010) or few basal dates (Korhola et al., 2010; Ruppel et al., 2013). Korhola et al. (2010) and Ruppel et al. (2013) reconstructed large scale peatland expansion based on the frequency of basal dates in sites with a minimum of three available dates, and were able to estimate peatland area increase by lateral expansion separately from peat initiation. Nevertheless, these methods still relied on the original sampling strategies of multiple basal dates from individual peatlands, which ideally should be random or cover the whole peatland, otherwise a sampling bias is introduced (Yu et al., 2013). Research like this study, which reconstructs lateral expansion of individual peatlands based on many basal dates and local topography, could be used to verify large scale peatland expansion reconstructions. The uncertainty in lateral expansion estimations could be decreased by obtaining a larger number of basal dates that cover the entire peatland area, including the margins. When there are sufficient detailed reconstructions of lateral peatland expansion available in a single region, these might be used to parameterize a model that describes the Holocene peat area based on local climate and topography.

This study highlights the within peatland variability in succession processes and response to varying conditions. Based thereon it is recommended that multiple peat cores per site are investigated before conclusions are made on the palaeoecology of any individual peatland. Ideally multiple different proxies, e.g. testate amoebae and plant macrofossils (cf. Loisel and Garneau, 2010), would be studied in tandem to reconstruct past conditions.

The method of reconstructing past CH_4 emissions using a plant macrofossil transfer function is a promising tool for the assessment of past C dynamics and climate - peatland feedback mechanisms, although the output uncertainties are still large. The accuracy and precision of this method would undoubtedly benefit from a larger training set with measurements of vegetation assemblages and CH_4 flux. It is important that the training set would contain CH_4 flux data averaged over multiple years in order to approximate the time scales on which the vegetation assemblages react to changing conditions. CH_4 flux reconstructions could also benefit from the addition of reconstructed moisture conditions, e.g. based on testate amoebae, as a predictive factor in the transfer function.

This study suggests that C accumulation in fens might decrease as a response to increased dry conditions or frequent occurrences of extreme dry weather. Temperatures and extreme weather conditions will probably increase in northern high latitudes in the future (IPCC, 2013; Fischer and Knutti, 2014), and this might have a large effect on northern fens (Fan et al., 2013). Fens seem to be more sensitive to changing moisture conditions than bogs (Gong et al., 2013), and fens are among the highest CH_4 emitting peatland types (Turetsky et al., 2014). Since a large part of northern peatlands are fens, it is essential that both bog and fen C dynamics are included in global C balance models (e.g. Spahni et al., 2013).

Furthermore, long term monitoring of C dynamics in drained peatlands could provide valuable information indicating whether these peatlands have a positive or negative effect on RF in the long term.

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